

# Natural enemy-mediated indirect interactions among prey species: potential for enhancing biocontrol services in agroecosystems

Anaïs Chailleux,<sup>a,b,c</sup> Emily K Mohl,<sup>d</sup> Mickaël Teixeira Alves,<sup>a,e,f</sup>  
Gerben J Messelink<sup>g</sup> and Nicolas Desneux<sup>a\*</sup>

## Abstract

Understanding how arthropod pests and their natural enemies interact in complex agroecosystems is essential for pest management programmes. Theory predicts that prey sharing a predator, such as a biological control agent, can indirectly reduce each other's density at equilibrium (apparent competition). From this premise, we (i) discuss the complexity of indirect interactions among pests in agroecosystems and highlight the importance of natural enemy-mediated indirect interactions other than apparent competition, (ii) outline factors that affect the nature of enemy-mediated indirect interactions in the field and (iii) identify the way to manipulate enemy-mediated interactions for biological control. We argue that there is a need to increase the link between community ecology theory and biological control to develop better agroecological methods of crop protection via conservation biological control. In conclusion, we identify (i) interventions to be chosen depending on agroecosystem characteristics and (ii) several lines of research that will improve the potential for enemy-mediated indirect interactions to be applied to biological control.

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**Keywords:** apparent competition; generalist predator; pest management; conservation biological control; functional biodiversity; ecosystem services

## 1 INTRODUCTION

Indirect interactions have the potential to occur in any community of three or more interacting species,<sup>1,2</sup> and complex interactions, including both direct and indirect effects, occur in natural and agricultural ecosystems.<sup>3</sup> By contrast to interactions like predation and symbiosis that involve contact between species, indirect interactions occur between two species that can be separated in time or space and require at least one additional mediating species.<sup>4,5</sup> Indirect interactions among species occur not only between trophic levels, in the form of bottom-up and top-down effects mediated through trophic cascades,<sup>6–10</sup> but also within trophic levels via resource competition<sup>11</sup> and/or shared predation.<sup>4,12</sup> In simple models,<sup>4</sup> prey species that do not directly interact can still negatively affect each other through interactions with a shared natural enemy (NE). This phenomenon is called apparent competition, because the dynamics of the two prey resemble that of prey competing for resources.<sup>4</sup> Indirect interactions often strongly affect food web structure,<sup>13</sup> and such interactions can generate both short-term effects on species abundance and long-term effects on population dynamics.<sup>5,14,15</sup>

Insect NEs of agricultural pests provide key biocontrol services in agroecosystems worldwide,<sup>16–19</sup> so NE-mediated indirect interactions have practical consequences.<sup>20</sup> Plant- and/or natural-enemy-mediated indirect interactions between herbivores have been increasingly reported in agroecosystems.<sup>21–26</sup> These indirect interactions between pest species may be positive or negative and symmetric or asymmetric. The net impact of NEs on pest dynamics depends on the direction, intensity and

duration of direct and indirect interactions among prey and their shared NEs.

Although biological control is founded on the concept of trophic cascades, it has rarely been implemented on the basis of indirect interactions within a trophic level. However, results of many studies may be interpreted in light of NE-mediated indirect interactions. For example, high arthropod diversity has been shown to enhance NE populations, resulting in increased biocontrol services on target pests in large-scale field studies.<sup>27,28</sup> In more focused experiments, the presence of alternative prey may increase control of pest species by generalist predators under field and semi-field

\* Correspondence to: Nicolas Desneux, French National Institute for Agricultural Research (INRA), UMR1355-ISA, 400 route des chappes, 06903 Sophia-Antipolis, France. E-mail: nicolas.desneux@sophia.inra.fr

a French National Institute for Agricultural Research (INRA), UMR1355-ISA, Sophia-Antipolis, France

b InVivo AgroSolutions, Paris, France

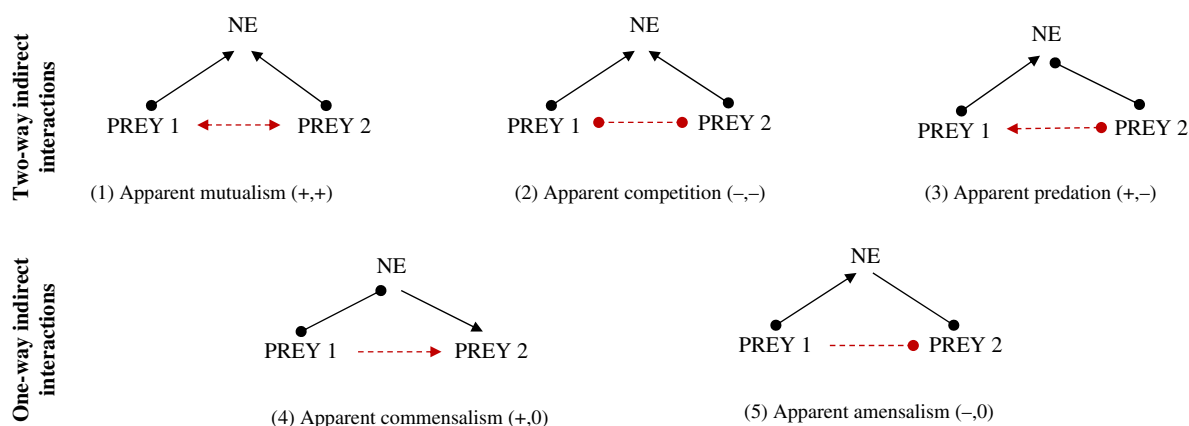
c CIRAD, UPR HortSys, Montpellier, France

d Department of Ecology, Evolution and Behavior, University of Minnesota, Saint Paul, MN, USA

e BIOCORE, INRIA, Sophia-Antipolis, France

f Department of Mathematical Sciences, University of Bath, Bath, UK

g Wageningen UR Greenhouse Horticulture, Bleiswijk, The Netherlands



**Figure 1.** Summary of types of indirect interactions between two prey species with a shared natural enemy (NE). Lines with arrows indicate a positive effect in the direction of the arrows, and lines with circles indicate negative effects in the direction of the circles. Solid lines indicate direct interactions, and dashed lines indicate NE-mediated indirect interactions.

conditions.<sup>26,29–33</sup> Overall, maintaining simultaneously low densities of various pests should theoretically promote the persistence of NEs through apparent competition.<sup>16</sup> However, the presence of several pests does not always result in NE-mediated indirect interactions;<sup>15,34,35</sup> the nature of indirect interactions primarily depends on specific species traits.

In this review, we argue that, although it is now obvious that NE-mediated indirect interactions contribute to pest population dynamics, insufficient efforts have been made to generate predictions that would facilitate the use of indirect interactions in biological control. Integrated pest management (IPM) practitioners need sophisticated ecological tools that utilise the functional characteristics of agroecosystems to predict the sign and strength of indirect interactions. Indirect interactions are known and described, and general theories explaining indirect interaction mechanisms exist, but now we need to link pest management (via biological control) and community ecology theory. In this review we aim to establish the first links between the ecological theory of indirect interactions and the practice of pest management via biological control.

## 2 THE NATURE OF INDIRECT INTERACTIONS

### 2.1 Overview

Depending on the temporal or spatial scale, the behaviour of prey and NEs involved and the quality and density of prey (affecting NE numerical response), the NE-mediated indirect interactions can take different forms.<sup>36</sup> Prey that interact through shared predators may have one- or two-way interactions with each other, and the effects may be either positive or negative (Fig. 1). Apparent competition ( $-,-$ ) and apparent mutualism ( $+,+$ ) are two-way indirect interactions (symmetrical interactions) that can occur between prey sharing a common NE; conversely, apparent amensalism ( $-,0$ ) and apparent commensalism ( $+,0$ ) are one-way indirect interactions (asymmetrical interactions) that occur when only one prey indirectly affects the other. In addition, NE-mediated apparent predation between two prey ( $+,-$ ) may occur,<sup>4,37</sup> particularly when interactions are considered over different timescales (Fig. 1).

Negative indirect interactions typically occur when alternative prey increase the abundance or density of a NE (numerical response or aggregation), resulting in increased consumption of the target prey. Positive indirect interactions typically occur in the absence of a numerical response or aggregation, or

through satiation and prey preference when an alternative prey reduces encounter rates between the NE and target prey. Mechanisms for one-way indirect interactions may include differences in the numerical response caused by the prey quality (see Section 2.2), important differences in population sizes of the two prey (see Section 2.3) or NE preferences<sup>38</sup> (see Section 4.1), among others.

Empirical studies frequently do not fully test the reciprocity of the interactions between prey.<sup>22,36</sup> For example, Muller and Godfray<sup>39</sup> manipulated grass aphid densities and measured the effects on out-planted nettle aphid densities, but they did not test for reciprocal effects of nettle aphids on grass aphids. However, possible asymmetry of indirect interactions (one-way) has important basic and applied implications. For biological control, it is crucial to know whether alternative prey will negatively affect the target prey population or not.

### 2.2 Role of prey quality

As described above, one of the conditions for apparent competition is the capacity of both prey species to support a numerical response of a shared NE. However, differences in the numerical response could occur, depending on the quality of the prey,<sup>40–42</sup> and lead to one-way NE-mediated interactions. If one prey allows a numerical response of a shared NE and the other one does not, the latter species will have no effect on the former, resulting in apparent amensalism. For example, the field study of Pons *et al.*<sup>43</sup> reported that some heteropteran predators do not respond numerically to *Therioaphis trifolii* and *Aphis craccivora* on alfalfa, suggesting that these species will not reciprocally interact with other prey via heteropterans.

Higher equilibrium densities of NEs through apparent competition may not be caused by increased prey availability alone, but may also result from diet mixing. It has been shown that juveniles of the predatory mite *Amblyseius swirskii* survive and develop better on a mixed diet of thrips and whiteflies than on a single diet of either of these species. Thus, thrips may promote control of whiteflies because diet mixing increases the predator numerical response to whiteflies without generating a reciprocal effect on thrips.<sup>32</sup> So far, this aspect of mixed diets has been ignored in theoretical models about indirect interactions, but may be important to integrate in theoretical tools aiming to optimise biological control programmes.

### 2.3 Role of prey density

Apparent commensalism may occur when one prey reduces predation on another one in an asymmetrical fashion, which often has negative consequences for biological control. Short-term apparent commensalism was observed in tomato crops where the mirid predator *Macrolophus pygmaeus* was found less effective to reduce population growth of the whitefly *Bemisia tabaci* in the presence of the invasive pest *Tuta absoluta* than when *B. tabaci* was alone.<sup>26,44</sup> However, the effect appeared to be mostly one way, in that *B. tabaci* had a low effect on predation on *T. absoluta*. This study suggested that prey abundance (and related prey–predator encounter rate) or availability (exposure to predation) may favour one-way interactions (at least in the absence of marked predator aggregation, see Section 3.1). However, the outcome at larger scales (spatial and temporal) could be drastically different.<sup>26</sup>

One-way indirect interactions driven by differences in abundance across prey species appear to have a strong influence on the structure of host–parasitoid communities<sup>45,46</sup> where two-way links in quantitative food webs are rare but one-way links from common to rare prey species are more frequent. Note that food webs are essentially observational, and experiments to test their predictions are recommended.<sup>15</sup> However, if relative prey abundance frequently generates one-way indirect interactions, pest management programmes relying on conservation biological control may require significant action promoting alternative prey. At the same time, the impacts of alternative prey are likely to change over the short- and long-term.

## 3 SHORT-TERM VERSUS LONG-TERM INTERACTIONS

Short-term NE-mediated interactions occur faster than one NE life cycle, and long-term interactions occur over timeframes longer than one NE life cycle. Given the long generation times of many NEs relative to their prey, the original concept of apparent competition that focused on the numerical response of food-limited predators may not explain many observations about the way NEs can influence the structure of communities. In theory, both short- and long-term indirect effects of shared NEs can lead to positive and negative NE-mediated indirect interactions.

### 3.1 Short-term indirect interactions

Short-term interactions usually occur within a single generation as a result of satiation, switching behaviour and/or prey preference in the shared natural enemy.<sup>14,47</sup> Many studies have shown reduced predation rates on a target pest in the presence of alternative prey, resulting in short-term apparent mutualism or commensalism.<sup>23,48–51</sup> Short-term apparent mutualism occurs through a dilution of encounter rates between prey and NEs, notably when NEs settle in prey patches independently of prey density and when they show a time-limited functional response.<sup>52</sup> Alternatively, apparent commensalism may occur at a short-term scale owing to differences in prey abundance or availability causing a one-way dilution effect; this may occur only when the NE does not aggregate on high prey density.<sup>53–55</sup> Commensalism occurs also when a NE encounters toxic prey on a plant and departs before consuming other, palatable, prey.<sup>56</sup>

Negative interactions may also arise at short timescales. For example, alternative prey may increase NE foraging activities and/or aggregation<sup>57</sup> (see Section 4.1). Apparent competition may be observed not only in the long-term with NEs that undergo a

numerical response but also in the short-term if the NE is an optimal forager and prey are limited in number. This is because NEs will aggregate to and stay longer in a patch where there are more prey, ultimately exploiting both prey species more than if each had been alone at a lower density.<sup>58</sup>

### 3.2 Long-term indirect interactions

Even when a short-term interaction occurs between two prey, food-limited NEs should eventually cause a long-term negative indirect interaction between prey owing to the numerical response of NEs.<sup>26,29,32,33,59,60</sup> This interaction results from the same mechanism observed when practitioners feed NEs with pollen or artificially produced eggs<sup>61,62</sup> (see Section 5.1). Liu *et al.*<sup>30</sup> reported more effective control of spider mites in apple orchards in the presence of both a predator and alternative prey than in the presence of a predator alone. The effects of the alternative prey on predator numerical response were detectable within a week of predator introductions, but differences in prey densities between treatments took more than a month to appear. Therefore, the numerical response of the predator may be observed more rapidly than the actual indirect interactions between prey.

Examples of short-term positive indirect interactions are relatively common (Section 3.1), but they have been mostly observed in studies where alternative prey were introduced into a controlled system with a limited number of predators, or where the behaviour of individual predators was measured. In such experiments, the main limitation was that the timescale of the experiments did not allow for a numerical response of the NEs. If NEs are not prey limited and exhibit satiation or switching behaviour, this can also lead to long-term apparent mutualism.<sup>14</sup> However, empirical evidence for this is limited (but see the article of Tack *et al.*<sup>15</sup>). Long-term apparent mutualism may also occur when population densities of one prey show cycles, resulting in repeated satiation of the shared predators and repeated reduced predation on the other prey.<sup>63,64</sup> However, further studies are needed to depict the precise nature of long-term indirect interactions in most empirical systems.

## 4 FACTORS AFFECTING INDIRECT INTERACTIONS: PREDATOR AND PREY BEHAVIOURS AND SCALES OF OBSERVATION

### 4.1 The effect of predator and prey behaviours

Predator and prey behaviours may modify the strength, the direction and the symmetry of indirect interactions. Behavioural changes in the way that two species interact through the presence of a third species are called trait-mediated indirect interactions<sup>34,56</sup> or functional indirect interactions,<sup>13</sup> although this last term is not widely used.

#### 4.1.1 Predator behaviour

NE preference for a given prey may arise (i) from a preference for particular species characteristics or (ii) from a response to prey densities, i.e. prey switching (a predator switches prey when its relative attack rate on a given prey type increases faster than the prey's relative abundance).<sup>65</sup> Many predators exhibit switching behaviours,<sup>66</sup> including those studied for biological control.<sup>44,67–70</sup> With either type of NE preference, the potential for negative indirect interactions to enhance biological control can be drastically reduced if NEs prefer the alternative prey (for predators<sup>23,47,71–74</sup>

and for parasitoids<sup>75,76</sup>). NE behaviour, when shaped by prey preferences, can induce one-way indirect interactions between prey (both apparent amensalism<sup>77,78</sup> and apparent commensalism<sup>56</sup>), sometimes favouring the pest. Predator preference is primarily determined by prey behavioural and physiological characteristics, such as (i) prey nutritive quality,<sup>35,73,79,80</sup> (ii) prey size or patch size,<sup>81</sup> (iii) prey mobility<sup>23,34,74,82</sup> or (iv) herbivore-induced plant volatiles.<sup>83–85</sup>

#### 4.1.2 Prey behaviour

Prey behaviour is a major factor that modulates NE-mediated indirect interactions among prey, notably in the short term. Indeed, prey can display various behaviours to avoid predation or parasitism, including settling in physical refuges,<sup>86–90</sup> fleeing a patch showing high predator density<sup>57,91</sup> and adopting defensive behaviours.<sup>92–94</sup> These behaviours can reduce encounter rates with predators and may ultimately lead to apparent amensalism, or even apparent predation, if the alternative prey remains available to the predators in the system.

### 4.2 Spatial scale of observation

The way NEs perceive the spatial distribution of shared prey can affect the predicted outcome of indirect interactions.<sup>12</sup> Experimental and observational studies of the effects of alternative food sources on biological control have occurred at a variety of scales, ranging from petri dishes to landscape-level manipulations. Perhaps not surprisingly given the complex nature of many indirect interactions, the spatial scale of the manipulation often appears to affect the nature of the indirect interactions observed.<sup>15,95</sup> For example, Ostman and Ives<sup>96</sup> found predator aggregation to aphids, but not planthoppers, in field studies, consistent with short-term apparent amensalism. However, they found short-term apparent commensalism in cage studies, where predators spent time on plants with pea aphids and neglected plants with potato leafhoppers.

## 5 APPLIED STRATEGIES

### 5.1 Alternative prey for early-season establishment

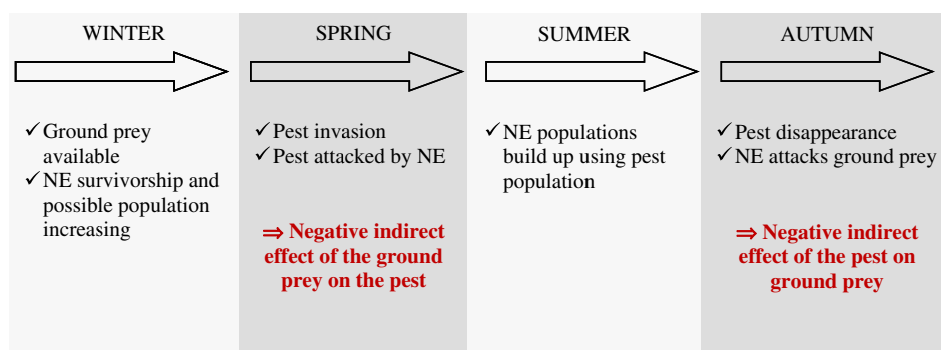
Alternative prey can help natural enemy populations establish in crops before pest arrival, notably early in the season. Temporal dissociation between natural enemy and pest arrival in crops can result in high NE densities relative to the density of the invading pest, thus preventing or delaying pest outbreaks.<sup>97,98</sup> For example, corn leaf aphids usually arrive early in the season on sorghum, and they support early population growth of coccinellids that

control economically damaging greenbugs later in the season.<sup>99,100</sup> In addition, when a targeted pest does not enable strong NE numerical response, NE population growth before pest arrival may increase the strength of biocontrol (see Section 2.2). Yoo and O'Neil<sup>101</sup> reported that the predator *O. insidiosus* showed a numerical response to thrips (alternative prey) but not to the aphid pest in soybean fields. However, thrips promote high predator densities early in the season that may reduce aphid populations later in the season.<sup>98</sup>

Introducing alternative prey early in the season could be a method to increase biological control by inducing apparent amensalism or apparent competition against a targeted pest.<sup>30,102</sup> In greenhouse crops, the manipulation of NE indirect interaction is easier because biotic and abiotic factors are better controlled than in open fields. This probably explains why temporal one-way indirect interactions are already used on occasion to enhance biological control in greenhouses. The 'alternative host and parasitoid in first' method involves introducing non-pest hosts on non-crop plants to maintain parasitoid populations in greenhouses where crops are going to be planted. If a targeted pest infests the crop, parasitoids can spill over from non-crop plants and parasitise target pest populations.<sup>28,103–105</sup> Similarly, the alternative prey can be replaced by an alternative food source; for example, sterilised *Ephestia kuehniella* eggs are used to promote mirid predator population growth in tomato crops early in the season.<sup>62</sup> However, this is not strictly a NE-mediated indirect interaction, as one of the 'prey' shows artificial population dynamics. Overall, these methods used in greenhouses generate the same patterns observed naturally in some fields: alternative prey or food sources promote NE population growth prior to pest outbreaks and increase biocontrol services.

### 5.2 Alternative prey to sustain natural enemies during low-pest-density periods

When alternative prey and pests do not co-occur in the habitat at a given time of the season, they can still interact indirectly at longer temporal scales (Fig. 2). Some predators require the presence of alternative prey in order to survive (or even develop, e.g. moulting) during periods when the target pest is absent.<sup>106</sup> Therefore, temporal separation between the pest and alternative prey may be helpful for biological control. This is particularly important in annual crops because the entire ecosystem is regularly disturbed. The availability of alternative prey in neighbouring habitats during non-cropping periods can maintain the predator population from one year to another. In addition, many generalist predators attack prey both on plants and on the ground. This broad diet enables predators to survive in fields on bare soils during



**Figure 2.** Example of possible mechanisms of apparent competition (–,–) between pest and alternative prey at the scale of 1 year in annual crops.



non-cropping periods and may ensure that they are present at the beginning of new cropping seasons. For example, predatory beetles survive from autumn until spring by feeding on lumbricid and collembolan prey in spelt<sup>107</sup> and spiders feeding on ground invertebrates in rice.<sup>27,108</sup> This suggests that soil and tillage practices that maintain alternative prey for NEs can benefit NE-mediated indirect interactions.<sup>109</sup>

Similarly, in perennial crops, like orchards, pests may not be available during particular periods of the season owing to pest and/or crop phenology.<sup>110</sup> The NEs may rely on alternative prey to sustain them during the non-pest periods of the year. For example, biological control of psyllids in pistachio crops in Turkey relies primarily on apparent competition with the leaf-curling aphid on almond trees, mediated by the predatory bug *Anthocoris minki*.<sup>111</sup> The leaf-curling aphid is a key alternative prey for the predator when pistachio psyllids are not available on pistachio trees in early spring. Similar findings have been reported for parasitoids of grape leafhoppers that diapause on alternative winter hosts on *Prunus* and *Rubus* plants during the winter in California.<sup>112–114</sup>

### 5.3 Alternative and target prey concurrently present in the agroecosystem

When alternative and target prey concurrently interact, the outcomes of NE-mediated indirect interactions are more variable and harder to predict than they are when there is temporal dissociation between prey, in part because behaviour and other traits become more important (see Sections 2.2 and 4.1).

The spatial location of the two prey species may reduce the efficiency of negative indirect interactions. This is especially likely when the alternative prey is provided in or near crops using external subsidies like mulch or banker plants. Mulch may increase the availability of detritivores for omnivorous predators, resulting in improved biocontrol of herbivores on crops.<sup>115</sup> However, strategies to increase alternative prey densities do not always improve herbivore suppression. For example, alternative prey in mulch may draw predators away from pests in the plant canopy.<sup>116,117</sup>

With concurrent prey, NE preference may also modulate the outcome of NE-mediated indirect interactions (Section 4.1). Consequently, strategies relying on indirect interactions between co-occurring prey for biological control will require intimate knowledge of the species involved and clearly defined objectives. For example, it will be important to ask whether long-term or short-term effects are desired, and if a long-term effect is sought, whether a short-term mutualism or commensalism is acceptable for the producer? An alternative to developing plans that require such detailed knowledge is to increase agroecosystem biodiversity overall in the hope of improving ecosystem services. Indeed, NE-mediated indirect interactions are one of the mechanisms involved in the concept of 'functional biodiversity'.<sup>118,119</sup>

## 6 PREY EXCLUSION MEDIATED BY SHARED NATURAL ENEMIES

Apparent competition may affect prey population dynamics in the same way as resource competition,<sup>120</sup> and prey exclusion is a possible outcome if (i) predation is very high on one prey (overexploitation), (ii) there are no refuges for the prey that support the smallest NE population or (iii) the less competitive prey suffers other detrimental interactions, such as resource competition.<sup>12</sup>

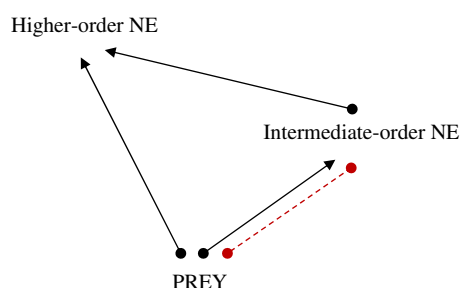
The presence of a prey species that supports high NE densities may promote overexploitation and potential exclusion of

alternative prey. Exclusion via apparent amensalism has been demonstrated empirically in a long-term population study in which prey species were not allowed to compete directly for resources.<sup>60</sup> Apparent competition could also theoretically lead to prey exclusion through destabilisation of the ecosystem; the introduction of a second prey species may increase overall availability of prey for an NE. Called the paradox of enrichment,<sup>121</sup> an increase in abundance of prey could favour NE–prey oscillations and may lead to prey extinction. However this phenomenon is rarely observed in ecosystems when both prey species are edible because either (i) the NE population density has a negative effect on its own per capita population growth rate via mechanisms other than prey depletion or (ii) a class of prey individuals shows low vulnerability to NEs.<sup>122</sup> The potential for prey exclusion via indirect interactions has important implications in the field of biological control but also in conservation biology. The possible impacts of indirect interactions on prey coexistence have been reviewed thoroughly in the field of conservation biology.<sup>123</sup> Notably, the authors stressed the negative role of one-way indirect interactions in endangered species conservation, and this may also be a risk when predators spill over from agroecosystems into smaller patches of native habitat. By contrast, possible pest exclusion through NE-mediated apparent competition (or other indirect interactions) has been rarely documented for biological control purposes.<sup>45,124</sup> Parasitoid-mediated apparent amensalism between two planthopper species excluded populations of one species more frequently than when populations were not exposed to apparent amensalism.<sup>124</sup> The hypothesis that apparent competition can lead to pest exclusion in agroecosystems has never been clearly demonstrated and deserves more attention from experimental field ecologists. However, even in the absence of complete exclusion, biological control may still be effectively achieved, and NE persistence in the agroecosystem improved.

## 7 NATURAL ENEMY INDIRECT INTERACTION VIA HIGHER-ORDER PREDATORS: RISKS AND POTENTIAL PITFALLS

Higher-order predation may intersect with apparent competition, so we briefly discuss how it can affect biological control in light of NE-mediated indirect interactions between prey. Cannibalism is defined as predation of conspecifics, hyperpredation is typically defined as NEs attacking other NEs without sharing prey and intraguild predation (IGP) is defined as predation by one species on interspecific competitors, which are designated as intermediate-order NEs. Hereafter, the term *higher-order predation* (HO predation) will be used to refer to both IGP and hyperpredation.<sup>8</sup> HO predators are relatively frequent in agroecosystems.<sup>125,126</sup> However, most higher-order NEs feed on intermediate-order NEs only when other prey are rare,<sup>127</sup> reducing the potential for HO predation to disrupt biocontrol services.<sup>128</sup> Additionally, most generalist predators are cannibalistic. Therefore, ecosystems with only one NE and one prey may include two prey types: conspecific and heterospecific prey. The effect of prey availability on cannibalism is particularly well documented in spider species.<sup>82,129–131</sup> As with HO predation, cannibalism decreases with the abundance of other heterospecific prey.

Over long timescales, juveniles (conspecific prey) or HO prey may generate a numerical response (or the survival) of the HO predators when primary prey are rare, ultimately negatively affecting the pests (apparent amensalism or apparent competition)



**Figure 3.** Indirect interactions involving a NE as prey through higher-order predation. Shown is an example of apparent competition between the target prey and the intermediate-order NE (intraguild prey) when sharing a higher-order NE. Lines with arrows indicate a positive effect in the direction of the arrows, and lines with circles indicate negative effects in the direction of the circles. Solid lines indicate direct interactions, and dashed lines indicate NE-mediated indirect interactions.

(see Fig. 3) and improving biological control.<sup>132</sup> However, HO predation and cannibalism can reduce the impact of predation on prey in arthropod communities because of suppression of the intermediate-order NEs (the HO prey and juveniles).<sup>25,71,133,134</sup> Such reduction may occur in spite of possible adaptive behaviours exhibited by HO prey/juveniles to avoid attack because such adaptive behaviours ultimately distract them from attacking their prey.<sup>135,136</sup> However, overall, the potential risk of HO predation disrupting biological control is thought to be relatively low.<sup>137–139</sup> Thus, cannibalism and HO predation could be expected to disrupt the efficiency of the HO prey/juveniles without a significant reduction in overall biological control services compared with those from a single NE alone. Moreover, HO predation may sustain NE populations over the long term when target prey populations are rare.

Finally, we can note that apparent competition may occur between two natural enemies via a hyperpredator. The existence of such interactions has been rarely studied (we found only one laboratory study<sup>140</sup>), even though many HO predators are known to prey on several NE species.<sup>25,127</sup>

## 8 MODELLING APPLICATIONS

Holt<sup>4</sup> described indirect effects in one-predator–two-prey systems using basic Lotka–Volterra types of model, and suggested the terminology of apparent competition. By modifying the assumptions about species behaviour and environmental conditions implicit in Holt's model,<sup>4</sup> a number of authors have explored a wide range of mechanisms that may alter the nature of indirect interactions.<sup>20</sup> Studies have investigated the impacts of saturating functional and numerical responses<sup>14,63,141–146</sup> (see Section 2.2), prey and predator behaviour<sup>14,147–153</sup> (see Section 4.1), spatial heterogeneity<sup>12,57,91,154</sup> (see Section 4.2), varying timescales<sup>57,155</sup> (see Section 3) and interference.<sup>14,146</sup> Many of these theoretical studies have predicted novel impacts of shared predation or have provided insight into potential biological mechanisms for patterns that could not have been detected or had been overlooked by empirical approaches.

However, these separate models fail to provide a unified theory that could easily be applied to a wide range of biological systems. One framework that holds potential to fill this gap is based on community modules,<sup>156,157</sup> which posit that multispecies communities can be described by an extension of pairwise interactions. These modules actually correspond to general patterns of interactions

within more complex systems composed of multiple trophic levels and interactions.

For instance, when simple rules can be derived in community modules, such as the  $R^*$  and the  $P^*$  rules (which predict that the competitor that can persist at the lowest resource level excludes the other) in the shared resource and shared predation modules respectively,<sup>11,120,158</sup> these allow for fundamental predictions about species dominance and indirect interactions. These rules are generated by comparing species equilibria in models that include or exclude an additional prey species, which is analogous to the way indirect effects are investigated in empirical studies.<sup>36</sup> However, their scope of application is currently limited: they are designed for extremely simple community models, which overlook most of the behavioural, temporal and spatial mechanisms influencing interactions and affecting predictions. Considering the substantial support that such rules could provide for optimising biological control programmes, significant tasks for future theoretical and empirical studies are (1) to develop key rules derived from community modules and (2) to identify critical assumptions underlying models of community interactions. The goal is to develop predictions for more complicated communities on the basis of simple variables, such as the relative abundance of prey species, their phenology and predator functional and numerical responses.

## 9 CONCLUSION AND PERSPECTIVES

Understanding how pests, alternative prey and NEs interact in complex and heavily managed environments such as agroecosystems is essential to the development of environmentally sound pest management methods in agriculture.<sup>19,159,160</sup> The current literature about NE-mediated indirect interactions among arthropods demonstrates that such interactions (i) are very frequent in agroecosystems and (ii) have a strong effect on pest, prey and NE population dynamics. Most indirect interactions appear to be one-way interactions. However, the reciprocity of indirect interactions has rarely been tested, as biological control-related studies are often most interested in one-way interactions, and it is more challenging to implement fully informative experimental designs. Additionally, positive indirect interactions are most likely to occur over short timescales, whereas negative indirect interactions often require longer timeframes to allow for a numerical response of the NE. Nevertheless, certain NE foraging behaviours, such as aggregation to sites of high host density, may generate negative interactions in the short term.

In agroecosystems, in contrast to natural ecosystems, crop management techniques (e.g. mixed crops, banker plants, cover crops, etc.) strongly influence the type and strength of NE-mediated indirect interactions. Habitat management may not always demand a radical change in farming practices<sup>161</sup> and could be used to manipulate NE-mediated interaction. We summarise in Table 1 the agroecosystem characteristics and the corresponding practices that can influence NE-mediated indirect interactions in managed agricultural ecosystems. Importantly, biological control may often benefit from indirect interactions that account for temporal variability in pest abundance, but outcomes are more variable when alternative prey coexist and share predators with pests at the same time.

We claim that a strong link should be created between community ecology theory and IPM practices to allow practitioners to use

**Table 1.** Summary of potential human interventions to enhance biological control, and their consequent effects on NE-mediated interactions, in relation to ecosystem item characteristics

	Item characteristics	Potential interventions	Effects on NE-mediated interactions
Plants	Presence of plant-provided food		Enhanced NE survival and numerical response
	Presence of prey refuges	Plant cultivar choice	Sustains food sources for the NE
	Plant cultivars releasing volatiles in response to herbivores	Releasing NE trained to respond to herbivore-induced plant volatiles	Enhanced the NE efficacy
Natural enemies	Behaviour (prey preference)	Choice of NE to release	Enhanced NE efficiency
	Numerical response	Addition of artificial food	Increased NE density
	Higher-order NE	Choice of NE to release	Limited negative interactions between NEs
	Nutritious value	Adding banker plants attracting high-quality prey	Enhanced NE numerical response
Prey	Phenology	Introducing alternative prey prior to pest arrival	
	Behaviour	Adding plant species that are repellent to herbivores	Negative (reduced prey host availability) or positive (maximised predation on fewer pests) effects
Agroecosystem	Plant diversity	Adding banker plants	Enhance prey diversity for the NE
		Adding intercropping	
		Mixing crop	
	Soil fauna	Soil practice choice: no-tillage practices	
	Perennial crop	Adding intercropping	
	Annual crop	Adding cover crop	

indirect interactions, especially apparent competition and apparent amensalism, to improve crop protection. Similarly to the development of pest thresholds for insecticide use, we argue for the development of practical tools that define the conditions under which indirect interactions can be beneficial, and which actions should be carried out by practitioners. Applied models, as already used for pesticides in IPM programmes, will be an essential tool to integrate indirect interaction manipulations into IPM programmes (e.g. see Section 8).

Our review highlights some initial conditions and possibilities for using indirect interactions to enhance biological control. Firstly, indirect interactions may rarely lead to pest suppression; therefore, they could not be used to control disease vectors in crops. Secondly, indirect interactions are more likely to occur in a diversified environment but will be easier to manipulate in a controlled agroecosystem; thus, manipulation is more likely to occur via an increase in the general biodiversity in open field and via precise manipulations in protected crops. Additionally, the use of NE-mediated indirect interactions is easiest when there is a temporal dissociation between the two prey (see Sections 5.1 and 5.2), so this should be the first approach for developing applied strategies. Because crop combinations at a field or regional scale have the potential to affect indirect interactions, another research priority should be to identify crops that do not share pests but that support pests that share natural enemies (see Sections 3.2 and 5.3). Finally, attempts to choose banker plants or cover crops to facilitate alternative prey in agroecosystems should include three main criteria: (1) the alternative prey is not a pest for the crop; (2) the alternative prey supports predator reproduction; (3) in the case of simultaneous

presence, the alternative prey is less preferred by the predator than the targeted pest (see Sections 4.1 and 5.3). These approaches should provide initial recommendations to help practitioners use NE-mediated indirect interactions to improve crop protection.

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